Photosynthesis: Carbon fixation reactions

Slide 2  Refresh your memory on the two stages involved in the overall process of photosynthesis. During the first stage, the light reactions which take place in the thylakoid membranes, convert solar energy into the chemical energy of ATP and NADPH. In the second stage of photosynthesis these energy molecules are used to fuel the reduction of carbon dioxide to sugars during the Calvin cycle. These carbon reduction reactions take place in the stroma of the chloroplast.

Slide 3  Carbon is available to the plant in the form of carbon dioxide from the atmosphere, or dissolved in the surrounding water for aquatic plants, algae and cyanobacteria. The Calvin cycle has three distinct stages: in stage 1 (carbon fixation), carbon dioxide is covalently bonded to the starter molecule or “fixed”. The starting molecule in the Calvin cycle is a 5-carbon sugar, ribulose 1,5-bisphosphate (RuBP). The reaction is catalyzed by the enzyme, Rubisco. In stage 2 (carbon reduction reactions), a series of reduction reactions take place. This is where most of the ATP and NADPH produced during the light reactions is used. In the third stage (regeneration), the starter molecule is regenerated. The Calvin cycle is similar to other metabolic cycles in that with each turn of the cycle the starting compound is regenerated. Now, let’s look at what happens at each stage in a little more detail.

Slide 4  During the first stage of the cycle, carbon dioxide enters the cycle and is covalently bonded to ribulose 1,5-bisphosphate producing an unstable 6-carbon molecule which is subsequently hydrolyzed to produce two molecules of the three carbon compound 3-phosphoglycerate (PGA or 3PG). The initial fixation reaction is catalyzed by the enzyme Rubisco (RuBP carboxylase/oxygenase) which is exhibiting carboxylase activity in this reaction. Rubisco is the world’s most abundant enzyme representing up to 40% of the total soluble protein of most leaves. Recall that 3-phosphoglycerate is one of the twelve key intermediates required for life. (Lesson1, module 1)

Slide 5  In the second stage of the cycle, each molecule of 3-phosphoglycerate is phosphorylated using ATP produced during the light reactions. This intermediate compound is then reduced to glyceraldehyde-3-phosphate (PGAL or G3P) using NADPH that was also produced during the light reactions. During each turn of the cycle one carbon molecule is fixed. So, THREE turns of the cycle are required to produce one three carbon molecule of glyceraldehyde-3-phosphate (PGAL or G3P). This three carbon molecule leaves the cycle and is further synthesized into sugars, starch and other organic molecules.
During the third stage of the Calvin cycle, 5 molecules of the three carbon molecule, glyceraldehyde-3-phosphate (PGAL or G3P), go through a series of reactions where the carbon molecules are reshuffled to produce five carbon molecules of ribulose 1,5-bisphosphate, which are necessary to begin the cycle again. Are you wondering why five molecules of glyceraldehyde-3-phosphate? Remember, three turns of the cycle are necessary to produce one three carbon molecule of glyceraldehyde-3-phosphate. The number of carbon molecules going through THREE turns of the cycle can be summarized as follows:

Stage 1, Fixation: \([\text{three, } 5C + \text{three, } 1C] \rightarrow \text{[three, } 6C] \rightarrow \text{[six, } 3C]\) molecules

Stage 2, Reduction: \([\text{five, } 3C + \text{one, } 3C]\)

Stage 3, Regeneration: \([\text{five, } 3C \rightarrow \text{three, } 5C]\) molecules

This figure summarizes all three stages of the Calvin cycle. Note the important molecules in the cycle: ribulose 1,5-bisphosphate (5C); 3-phosphoglycerate (3C); glyceraldehyde-3-phosphate (3C). When the enzyme Rubisco carboxylase catalyzes the reaction between carbon dioxide and ribulose 1,5-bisphosphate, the carbon from carbon dioxide is fixed into another molecule, subsequently producing 3-phosphoglycerate, during the first stage of the cycle. ATP and NADPH are used during the second stage during the reduction reactions to produce glyceraldehyde-3-phosphate. ATP is also used during the regeneration stage where ribulose 1,5-bisphosphate is regenerated. For every three turns of the cycle, one molecule of glyceraldehyde-3-phosphate (3C) leaves the cycle to be further synthesized into sugars and other macromolecules needed for cellular metabolism.

Glyceraldehyde 3-phosphate (PGAL or G3P) leaves the Calvin cycle to be further metabolized into sugars and starches which are eventually used for energy production during cellular respiration in the mitochondria. This figure shows how some of the intermediate products of the Calvin cycle are also metabolized into different macromolecules within a plant cell and how many of the processes within a cell are interconnected.

Recall that the enzyme Rubisco has both carboxylase and oxygenase activity. This means that carbon dioxide and oxygen compete for the binding site of the Rubisco enzyme. When carbon dioxide concentrations are high, carboxylase activity of the enzyme is favored and the Calvin cycle proceeds as previously discussed. However, when the concentration of carbon dioxide inside the leaf begins to fall, oxygenase activity of the enzyme is favored. As you can see in this figure, when the oxygenase activity of Rubisco is favored only one molecule of 3-phosphoglycerate is produced. If this process of photorespiration continues it causes a reduction in the production of sugars and other organic molecules necessary for plant growth resulting in slower growth of the plant. This may occur for example, on a hot day or during dry conditions when stomata close in order to conserve water subsequently causing increased levels of oxygen (produced during photosynthesis) in the leaf tissue. Photorespiration is avoided in two other
metabolic pathways that have evolved: the C4 and crassulacean acid metabolism (CAM) pathways.

**Slide 10** Plants which exhibit initial carbon fixation using the enzyme Rubisco are referred to as C3 plants, since the first product of carbon fixation is a 3-carbon sugar. Some plants have eliminated photorespiration and as a result, have become more efficient in carbon fixation. One such group of plants is referred to as C4 plants. C4 plants use the enzyme phosphoenolpyruvate (PEP) carboxylase to initially fix carbon in the mesophyll cells into a four carbon compound. The four-carbon organic acid is transported to specialized cells called the bundle sheath cells, where it is decarboxylated to produce a three-carbon molecule that is recycled back to the mesophyll cells, and carbon dioxide. The carbon dioxide is now fixed by Rubisco carboxylase and reduced to sugars via the Calvin cycle in the bundle sheath cell. You have probably worked out the overall advantage of this mechanism. The Calvin cycle proceeds in an area of plant tissue which constantly has a high concentration of carbon dioxide, thereby preventing the oxygenase activity of Rubisco. This specialization separating the location of the initial fixation of carbon dioxide and the location of the Calvin cycle presents a more efficient system to reduce carbon dioxide. Examples of C4 plants include *Poinsettia*, lamb’s-quarters, pigweed and many of the tropical grasses including corn, sugar cane and sorghum.

**Slide 11** Crassulacean acid metabolism (CAM) plants have a different strategy to promote a high concentration of carbon dioxide in the vicinity of the Calvin cycle, ensuring the carboxylase activity of Rubisco. These plants open their stomata at night and close them during the day, the opposite to most plants that we learn about. Many of these plants are succulents growing in arid conditions. Opening stomata at night when it is cooler helps the plant conserve water. When carbon dioxide enters through the plant stomata at night it is incorporated into an organic acid, a reaction that is catalyzed by the PEP carboxylase enzyme. The organic acid, malic acid, is stored in the vacuole of the mesophyll cells overnight. During daylight hours, the malic acid is recovered and undergoes decarboxylation to produce a three-carbon molecule and carbon dioxide. The Calvin cycle proceeds during daylight hours incorporating carbon dioxide into sugars and other organic molecules. This is why if you were to taste one of these plants in the evening it tastes sour; taste the same plant at mid-day and it tastes sweeter. During decarboxylation the stomata are closed so the concentration of carbon dioxide builds up in the plant cells. Again, this ensures the carboxylase activity of Rubisco and the Calvin cycle operates efficiently reducing carbon dioxide to sugars. Both of these reactions take place in the same cell but are separated by the day/night cycle. Examples of CAM plants include cacti and many succulents, pineapple and some orchids.